ADDITIONAL MATERIAL OF *ANHINGA GRANDIS* MARTIN AND MENGEL (AVES: ANHINGIDAE) FROM THE LATE MIOCENE OF FLORIDA

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Abstract. — An associated partial skeleton and other previously unknown skeletal elements of *Anhinga grandis* Martin and Mengel, 1975, are described from three late Miocene (latest Clarendonian and early Hemphillian) localities in Florida. Derived osteological characters of the tarsometatarsus show *A. grandis* to be more closely related to the New World *A. anhinga* than to the Old World *A. rufa, A. melanogaster,* and *A. novaehollandiae.* The wing of *Anhinga grandis* was larger than that of the largest living species, *Anhinga novaehollandiae,* but the pelvic limb was comparable to that species in size.

Anhinga grandis was originally described from a single distal end of a humerus from the late Miocene Cambridge (=Ft.-40) local fauna, "Kimball" formation, Frontier County, Nebraska (Martin and Mengel 1975). The associated mammalian fauna, along with that from several other local faunas in western Nebraska, were used to typify a discrete post-Hemphillian, pre-Blancan Land Mammal Age, termed the "Kimballian" (Schultz et al. 1970). Subsequent work (Breyer 1981, Voorhies 1984) has demonstrated that no stratigraphic nor biochronologic evidence exists to support this proposal. The Cambridge local fauna is now considered to originate in the Ash Hollow Formation and to be early Hemphillian in age, about 8.5 MYBP (=million years before present) (Tedford et al., in press).

This paper describes new material referable to *Anhinga grandis* from three late Miocene localities that extends the range of the species to Florida and provides additional data on its morphology and systematic relationships to other species in the genus *Anhinga.*

Materials and Methods

Fossil specimens included in this study are housed in the Vertebrate Paleontology collections of the Florida State Museum (UF) and the University of Nebraska State Museum (UNSM). Modern comparative material came from the collections of Pierce Brodkorb; Florida State Museum (UF); National Museum of Natural History, Smithsonian Institution (USNM); American Museum of Natural History (AMNH); and Royal Ontario Museum (ROM). Modern species and number of specimens examined are as follows: *Anhinga anhinga* (17), *A. rufa* (10), *A. melanogaster* (1), *A. novaehollandiae* (1). Anatomical terminology follows Baumel et al. (1979) and Howard (1929).

Measurements given in Tables 1 and 2 are defined below.

HUMERUS: LENGTH—Greatest length from the head of the humerus through the midpoint of the lateral condyle. LATIS—Greatest length from the proximal-most extension of the tuberculum for the attachment of the posterior head of the latissimus dorsi through the midpoint of the lateral condyle. W-SHAFT—Transverse width of midshaft. D-SHAFT—Depth of midshaft. W-DIST—Transverse width of distal end from the entepicondylar prominence to the ectepicondylar prominence. D-DIST—Depth of distal end from cranial face of external condyle through ridge slightly mediad

from external tricipital groove, measured at right angles to the long axis of the shaft. D-ENTEP—Depth from attachment of the pronator brevis through entepicondyle, measured at right angles to the long axis of the shaft.

CARPOMETACARPUS: LENGTH—Greatest length from most proximal portion of the carpal trochlea through facet for digit III. W-CARPAL—Transverse width carpal trochlea measured at the proximal edge of the articular facet. L-MCI—Length metacarpal I from process of metacarpal I to pollical facet. D-SHAFT—Depth of midshaft of metacarpal II. W-SHAFT—Transverse width of midshaft of metacarpal II. D-DIST—Greatest depth of distal end, measured across dorsal edge of facet for digit II. W-DIST—Transverse width distal end from edge of facet for digit II through facet for digit III.

TIBIOTARSUS: W-SHAFT—Transverse width of midshaft. D-SHAFT—Depth of midshaft. W-DIST-CR—Transverse width of distal end, measured across cranial portion of condyles. D-MCON—Greatest depth of medial condyle. D-LCON—Greatest depth of lateral condyle.

TARSOMETATARSUS: LENGTH—Greatest length from intercondylar eminence through trochlea for digit III. W-SHAFT—Transverse width of midshaft. D-SHAFT—Depth of midshaft. W-PROX—Greatest transverse width proximal articular surface, measured across dorsal surface. D-PROX-M—Depth of proximal end, measured from dorsal edge of the proximal articular surface through the medial hypotarsal crest. W-DIST—Greatest transverse width of distal end.

SYSTEMATICS
Family Anhingidae Ridgway, 1887
Genus *Anhinga* Brisson, 1760
Anhinga grandis Martin and Mengel, 1975
Fig. 1A–H

*Holotype.*—UNSM 20070, distal end of left humerus, from the early Hemphillian

Cambridge local fauna, Frontier County, Nebraska.

Referred material.—From the Love Bone Bed local fauna, Alachua County, Florida: UF 25739, proximal end of right humerus; UF 25723, UF 25725, distal ends of right humeri; UF 26000, nearly complete right coracoid. Collected between 1974 and 1981 by personnel from the Florida State Museum.

From the McGehee Farm local fauna, Alachua County, Florida: UF 11107, distal end of right humerus. Collected June 1964 by R. Allen.

From the Haile XIXA local fauna, Alachua County, Florida: UF 61396, associated partial skeleton including the distal end of left humerus, right humerus missing proximal end, right ulna missing distal end, proximal end of right radius, right radial carpal, right carpometacarpus missing minor metacarpal, distal half of right tibiotarsus, distal half of left tibiotarsus (originally numbered PMW 1609–PMW 1616); UF 61399, complete right tarsometatarsus (PMW 1722). The associated partial skeleton was collected by Mr. George Heslop; other skeletal elements were collected by Mr. Phil M. Whisler (=PMW). All specimens of anhingas from Haile XIXA were generously donated to the Florida State Museum by Mr. Phil M. Whisler of Venice, Florida.

Age and horizon of referred material.—Late Miocene of Florida. The Love Bone Bed local fauna is latest Clarendonian in age, approximately 9 MYBP (Webb et al. 1981). Both the McGehee Farm local fauna and the Haile XIXA local fauna are early Hemphillian in age, approximately 8.5 MYBP (Hirschfeld and Webb 1968, Becker 1985). The Love Bone Bed and McGehee Farm local faunas originate in the Alachua Formation (Williams et al. 1977), the Haile XIXA local fauna is from unnamed sediments filling a solution cavity, now exposed in a limestone quarry. The determination of the relative ages of these local faunas are based on the biochronology of the included land mammals.
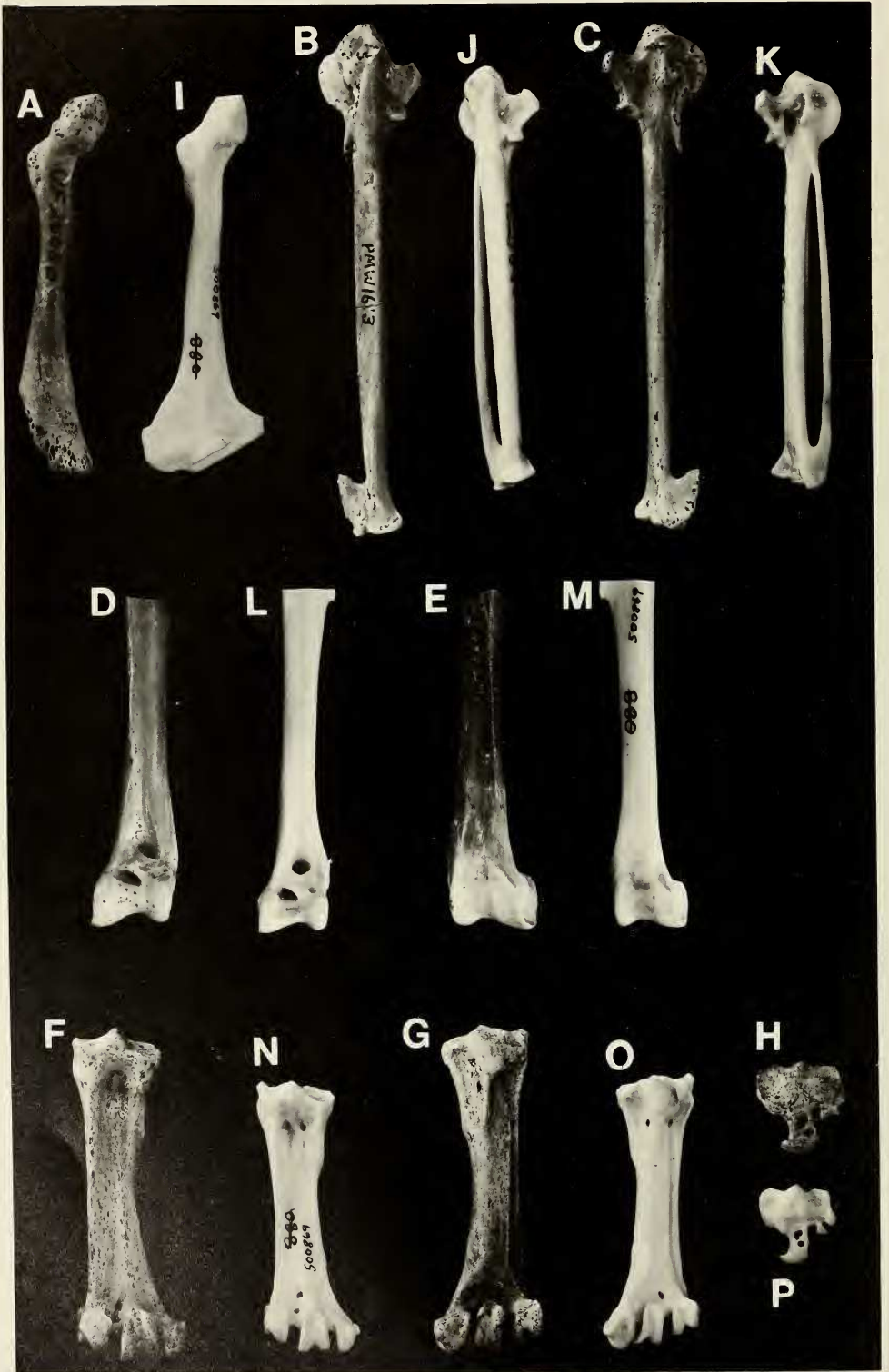
Description. — The referred coracoid (UF 26000) of *A. grandis* is abraded and little detail can be seen of either extremity. It appears to be comparable in size to that of *Anhinga novaehollandiae.*

In caudal view, the referred proximal end of the humerus of *A. grandis* (UF 25739) has a sharper caudo marginalis than in any living species and an inflated humeral head that blends smoothly with the shaft. The fossa pneumatotricipitalis has a heavy crus ventrale and the attachment for the posterior head of the latissimus dorsi is prominent. In cranial view, the angle between the sulcus ligamentosus transversus and the impressio m. coracobrachialis cranialis has a more rounded, less acute shape than that of the comparable structures in any living species of anhinga.

The distal end of the humerus of *A. grandis* agrees well with the holotype (USNM 20070) described by Martin and Mengel (1975), except that the holotype has a more robust shaft than in any of the specimens from Florida. One specimen (UF 61396, right humerus lacking proximal end) is sufficiently complete to estimate the total length of the humerus in *Anhinga grandis.* The length from the proximal extension of the tuberculum for the attachment of the posterior division of the latisimus dorsi through the distal end of the lateral condyle is approximately 85% of the total length of the element (Table 1). If a comparable ratio is assumed in *A. grandis,* then its humerus would have had an estimated length of 150 mm.

The referred partial ulna, proximal end of the radius, and radial carpal of *A. grandis* are much the same as in the living North American species of *anhinga,* only larger.

The referred carpometacarpus of *A. grandis* is comparable in length to that of *A. novaehollandiae* or *A. melanogaster,* but is slightly more robust. The fovea carpalis caudalis is deeper than in *A. anhinga,* but is comparable to that of *A. novaehollandiae* or *A. melanogaster.* Other qualitative features are within the range of variation seen in living species.

The distal end of the tibiotarsus of *A. grandis* is slightly larger than that of *Anhinga novaehollandiae* but differs from any living species by having the posterior rim of the medial condyle more medially flared.

The referred tarsometatarsus of *A. grandis* is slightly smaller than that of *A. novaehollandiae* and is generally less sculptured than that of the living species. The hypotarsus encloses two canals (as in *A. anhinga*) and agrees with *A. anhinga* in the relative position of a shallow groove on the medial border of the shaft. The intercondylar eminence is more prominent but the medial and lateral parahypotarsal fossae are less excavated, as in *A. anhinga.* The position of the distal vascular foramen is intermediate between the Old and New World Anhingas (placed higher on the shaft in *A. anhinga*; lower in *A. melanogaster* and *A. rufa*; absent in the single available specimen of *A. novaehollandiae*).

Discussion. — The fossil record and the systematic relationships of anhingas have been recently reviewed (Olson 1985, Becker 1986). Of the two species groups of living anhingas, *Anhinga grandis* can be shown to be a member of the group that includes the living North American *A. anhinga* by the possession of the (presumably) derived condition whereby two canals are enclosed within the hypotarsus and by the relative

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Fig. 1. Skeletal elements of *Anhinga grandis* (A–H) and *Anhinga anhinga* (I–P; USNM 500869). A, UF 26000, right coracoid; B–E, UF 61396, right carpometacarpus, distal end of left tibiotarsus; F–H, UF 61399, right tarsometatarsus; A, I, Ventral view; B, J, Dorsal (external) view; C, K, Ventral (internal) view; D, L, Cranial (anterior) view; E, M, Caudal (posterior) view; F, N, Dorsal (anterior) view; G, O, Plantar (posterior) view; H, P, Proximal end view. All photographs natural size.

Table 1.—Measurements of pectoral limb elements of *Anhinga anhinga* (N = 17, 5 males, 11 females, 1 unknown sex) and *Anhinga grandis*. Data are mean ± standard deviation, and observed range. (*) = holotype. See Materials and Methods section for definition of measurements.

	Anhinga anhinga	Anhinga grandis
Humerus		
LENGTH	125.09 ± 5.75	—
	113.2–137.6	
LATIS	105.14 ± 4.41	126.2
	98.6–112.5	
W-SHAFT	6.59 ± 0.35	9.6*
	5.9–7.3	8.3; 7.8; 8.0
D-SHAFT	5.84 ± 0.28	7.9*
	5.4–6.7	6.8; 7.0; 6.7
W-DIST	13.12 ± 0.98	15.9*
	12.0–14.9	15.0; 17.2; 16.0; 15.8
D-DIST	8.72 ± 0.35	11.4*
	7.9–9.3	10.5; 10.0; 10.2; 10.2
D-ENTEP	7.64 ± 0.52	[10.2*]
	6.5–8.7	9.4; 9.5; 9.0; 8.8
Carpometacarpus		
LENGTH	63.91 ± 2.45	74.8
	59.8–68.4	
W-CARPAL	6.15 ± 0.31	7.5
	5.7–6.9	
L-MCI	8.72 ± 0.51	9.6
	7.8–9.5	
D-SHAFT	3.71 ± 0.32	4.1
	3.1–4.4	
W-SHAFT	4.66 ± 0.43	5.0
	4.1–5.8	
D-DIST	5.02 ± 0.35	5.5
	4.3–5.7	
W-DIST	7.08 ± 0.34	7.9
	6.3–7.6	

Table 2.—Measurements of pelvic limb elements of *Anhinga anhinga* (N = 17, 5 males, 11 females, 1 unknown sex) and *Anhinga grandis*. Data are mean ± standard deviation, and observed range. See Materials and Methods section for definition of measurements.

	Anhinga anhinga	Anhinga grandis
Tibiotarsus		
W-SHAFT	5.16 ± 0.32	5.9; 6.5
	4.6–5.8	
D-SHAFT	4.15 ± 0.18	4.8; 5.4
	3.9–4.5	
W-DIST-CR	10.23 ± 0.37	11.4; 11.4
	9.6–10.9	
D-MCON	9.26 ± 0.35	11.1; 11.1
	8.8–10.0	
D-LCON	8.25 ± 0.33	9.4; 9.5
	7.8–8.9	
Tarsometatarsus		
LENGTH	40.68 ± 1.75	47.8
	37.8–44.9	
W-SHAFT	6.48 ± 0.35	7.8
	6.0–7.4	
D-SHAFT	3.91 ± 0.29	4.9
	3.5–4.5	
W-PROX	11.03 ± 0.53	12.8
	10.1–12.0	
D-PROX-M	11.91 ± 0.65	13.8
	10.7–12.8	
W-DIST	14.40 ± 0.57	16.5
	13.7–15.6	

position of a shallow groove on the medial border of the shaft (Harrison 1978).

The body size of fossil species can be estimated by a number of methods. Martin and Mengel (1975) estimated the mass of *Anhinga grandis* at 2.5 kg by comparison with the living North American anhinga, assuming that the width of the distal end of the humerus is isometrically proportional to body mass raised to the ⅓ power. However, the condition of isometric scaling of limb element width to body mass rarely oc-

curs in birds (Prange et al. 1979), and probably the body mass of *A. grandis* is overestimated by this method. Prange et al. (1979) note that the length (in mm) of the humerus squared is nearly directly proportional to body mass (in grams) in flying birds. If the length of the humerus of *Anhinga grandis* is assumed to be 150 mm, then this method would estimate the body mass of this species at 2.2 kg.

Another approach is to estimate the mass of *A. grandis* by direct comparison with a living species of anhinga of comparable size. The associated skeleton (UF 61396) has the carpometacarpus, distal end of the tibiotarsus, and the referred tarsometatarsus (UF 61399) all equal to that of *A. novaehollandiae* (AMNH 11479), suggesting that the

size of *A. grandis* was approximately equal to that of *A. novaehollandiae.* Serventy and Whittell (1976) report the weight of females of *A. novaehollandiae* as ranging from 1.67 kg to 2.04 kg ($\bar{x} = 1.84$ kg); 1.47 kg for one male. By this method, the weight of *A. grandis* would be estimated as 1.8 kg, or about 1.5 times the size of the living North American anhinga.

The humerus from the associated skeleton is relatively larger than that of *A. novaehollandiae,* although the other skeletal elements are comparable. This may suggest that the wing of *A. grandis* was proportionately larger than that of *A. anhinga,* or that it had a slightly larger body size. The tarsometatarsus of *Anhinga grandis* is less sculptured by muscle attachments than that of *A. anhinga.* In comparison with *A. anhinga, Anhinga grandis* was perhaps less adapted for perching and climbing about in vegetation and more adapted for soaring.

Acknowledgments

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